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the Atlantic Salmon Trust

The Behaviour of Adult Salmon (*Salmo salar* L.) in the River Tay as Determined by Radio Telemetry

John Webb

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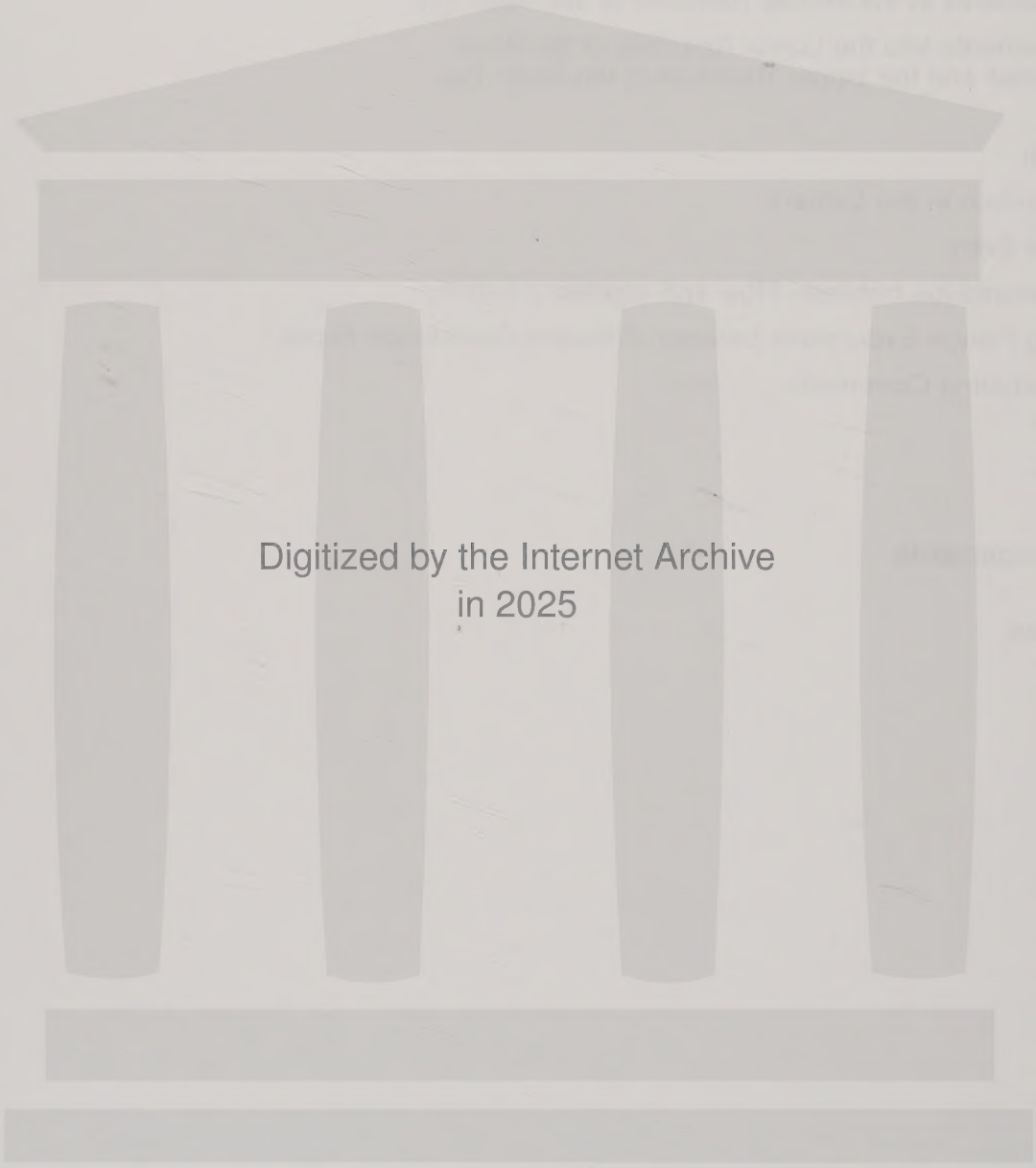

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The Behaviour of Adult Atlantic Salmon (*Salmo salar* L.) in the River Tay as Determined by Radio Telemetry

John Webb

Marine Laboratory, Aberdeen
(Employed by the Atlantic Salmon Trust)

Introduction

Over the course of the summer of 1987 and the spring and early summer of 1988, the Scottish Office Agriculture and Fisheries Department and the Atlantic Salmon Trust monitored the migratory behaviour of adult salmon entering the River Tay in eastern Scotland using radio telemetry. During the course of these studies, attention was focused on determining those factors that affected the migratory behaviour of salmon entering the river at different times of the year. The effect of levels and changes in the regulated main river and tributary flows was also monitored.

Webb (1989) described the movements of 22 radio-tagged grilse and salmon entering the River Tay during the summer of 1987. In a second report (Webb,1990), an account was given of the behaviour of a group of 11 radio-tagged salmon ascending to Pitlochry dam in the late spring of the following year.

In this final report, further information on the radio-tracking study undertaken in 1988 is given, when a further 22 salmon were tagged and their behaviour monitored up to the beginning of the spawning season.

Materials and Methods

The study was performed from April to late October 1988.

Fish were captured at two commercial net and coble fishery stations within the upper reaches of the River Tay estuary, near Perth. The methods employed in the selection of suitable specimens for tagging are described elsewhere (Webb,1989, 1990). Fish taken from both the Stock Green (The Tay Salmon Fisheries Company, Ltd) and the Ships fishing stations (Insch Fishing Company) were tagged and then released immediately above the highest operational limit of the Limie fishing station (The Tay Salmon Fisheries Company, Ltd). The positions of the net and coble fishing stations and the release areas are described elsewhere (Webb, 1989, 1990). For the purposes of description the names of the netting stations involved in the study are abbreviated as follows: SG (Stock Green), SPS (Ships), LE (Limie), TY (Tappy) and MY (Mary).

Details of the radio-tags used, the operation and deployment of the automatic listening stations (ALSTNs), the active tracking techniques and the methods of data collection are given by Hawkins and

Smith (1986) and Webb (1989, 1990). Daily tracking was carried out from the date when the first fish was released on the 24 April until 6 September. Periodic bank-side and aerial tracking took place up until 15 October. Passive monitoring by the ALSTN units continued in the area of the Tay/Isla and Tay/Tummel confluences until 15 October. The positions of the remaining tagged fish were noted on 31 October.

Radio-tagged fish were identified by their characteristic radio frequencies and signal pulse rates. Individual fish were assigned code numbers, ie F1, F2, etc. Rates of movement up and down stream (net ground speed) are based on calculations made on data derived from ALSTN units only which gives the most accurate indication of movement in either direction. The movements of fish are expressed in terms of the linear distance up stream from a standard datum point at Elcho Castle, near Perth (OS Grid Reference; 316441 721316) unless otherwise stated. The first stopping position within the lower reaches of the river is defined as the location at which tagged fish remained at a single location (± 0.5 km) for six hours or more after having ascended through the tidal limit at Scone. The upstream limit of the estuary is defined as the point to which the tidal influence on water level extends, and is located less than 0.5 km below the confluence of the River Tay and the River Almond, at Scone.

Discharge and water level data for the period of the study were provided by the Tay River Purification Board, Perth, data being used from the Ballathie (lower Tay), Caputh (middle Tay), Pitnacree (upper Tay), Port-na-Craig (River Tummel) and Almondbank (River Almond), Wester Cardean (River Isla) and Craighall (River Ericht) gauging stations. The positions of these gauging stations are shown in Figure 1.

Mean daily discharges ($m^3 s^{-1}$) are represented by the abbreviation MDD. Summary monthly average flows (calculated for the stations described for the periods 1958 to 1987 at Ballathie, Caputh and Pitnacree, and 1973 to 1987 at Port-na-Craig and Almondbank) are represented by the abbreviation % SMDD. This method of describing river flows allows levels of discharge at different times of the year to be considered in relation to the seasonal norm rather than as a proportion of the more commonly used annual summary (ie Q values).

Instantaneous levels of flow entering the upper estuary at Scone and the confluence at Logierait are calculated from gauged flows passing the Ballathie and Pitnacree gauging stations approximately six and three hours beforehand, respectively.

All the discharges quoted are with respect to the standard hydrological day (0900-0900 GMT) rather than a calendar day. Those periods corresponding to less than six hours of the respective hydrological day are expressed as a proportion of the level of flow recorded over the course of the previous daily period. The SMDD values for the seven gauging stations previously described are given in Table I.

For the purposes of description, flow conditions at the time of the movements of tagged fish through the tidal limit at Scone and past ALSTN units near confluence areas are abbreviated to four flow regime (FR) codes (see Tables II-IV) as follows:

S – movements during stable river flows (flows having remained stable for ≥ 24 h);

I – movement during period of increasing river flow (ie a spate);

DS – movement during flows associated with the decline in river flows in the aftermath of a spate;

D – movement during a decline in basal flows (a decline in seasonal basal flows not associated with a single or multiple spate event in the preceding 24 h).

FR were estimated from hydrographs recorded at

Table I
Summary of the long term monthly discharges (SMDD) recorded at the gauging stations described in the text. All flows described in $m^3 s^{-1}$

	Period	April	May	June	July	August	September
Ballathie	1958–1987	149	126	84.7	66.2	85.6	121.0
Caputh	1958–1987	119	102	68.6	54.5	69.1	100.0
Pitnacree	1958–1987	47	41	28.6	24.2	30.0	45.6
Port-na-Craig	1973–1987	61	49	30	26	33.6	53.6
Wester Cardean	1985–1989	12.7	10	5.3	5.8	12.1	11.7
Craighall	1972–1989	7.6	6	4	2.6	4	5
Almondbank	1973–1987	4	3	2	1.4	2.3	4

Ballathie, Caputh, Pitnacree and Port-na-Craig gauging stations (Fig. 1).

Results

Between late April and August 1988, 42 salmon were radio-tagged and released into the upper reaches of the Tay estuary. The migratory behaviour of 11 of the fish that subsequently entered the River Tummel and continued up stream to Pitlochry dam was described by Webb (1990). The present report describes the movements of the remaining 31 fish that were tagged and released over the same period. Tables II and III give details of those fish tagged and released in the upper reaches of the tidal estuary of the River Tay over the period 25 April–8 July 1988.

Of the 31 fish released, nine were recaptured by various net and coble stations operating in the upper reaches of the estuary (Tables II and III). One fish (F31) was recaptured seven days after being released, by an angler fishing at Ballathie (15/07/88).

Fourteen fish were tracked successfully through to spawning. The remaining seven were lost within the river during the latter part of the summer perhaps owing to tag failure.

Entry to the River

Twenty-two radio-tagged fish entered the river between 26 April and 8 July. Migration into the river from the upper reaches of the estuary took place over a range of flows corresponding to varying proportions of the long term seasonal flows (SMDD) recorded at Ballathie. These proportions corresponded to 95–113% SMDD (April), 57–112% SMDD (May), 44–112% SMDD (June) and 37–70% SMDD (July) (Tables II, III and IV).

Ten radio-tagged fish entered the river during the course of declining spate flows, and a further five entered during increasing main river flows. The entry of the remaining seven fish coincided with stable main river flows (Tables II, III and IV). Those fish that entered the river within eight hours or less of release, covered the 7 km between the release site and the tidal limit in 3.5 to 7.75 hours (mean, 5.3 hours). Their movement up stream corresponded to net ground speeds of approximately 21.6 to 48 km day^{-1} (mean, 31.6).

Tables II and III show the flows at entry to the river from the estuary. Movements to the Tay/Almond confluence at Scone were compared with prevailing main river flows but no significant relationships were found. Thirteen fish that entered the river moved up stream from the release site without delay, passing

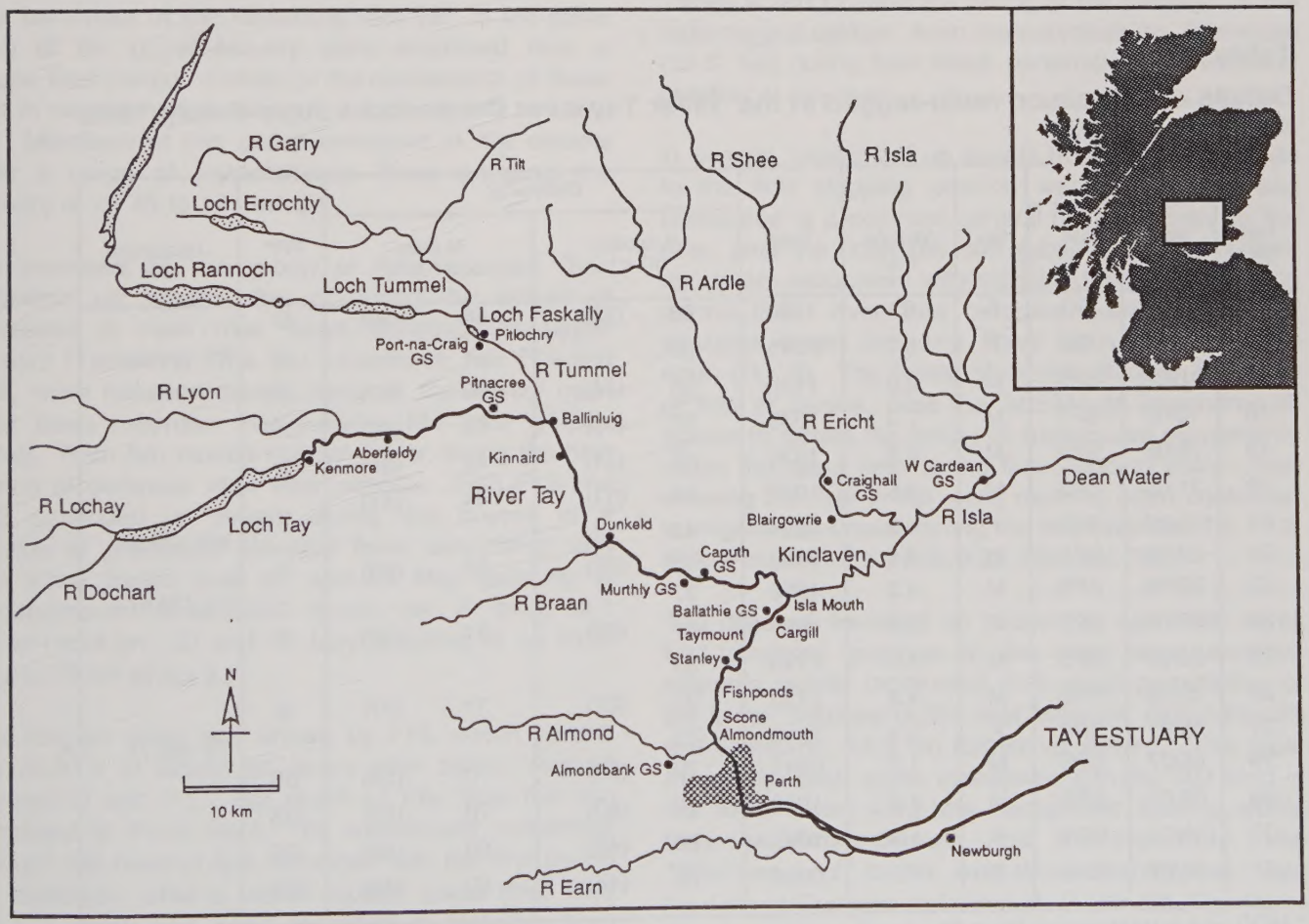

Figure 1. The River Tay catchment showing the main tributaries, lochs and the positions of the flow gauging stations (GS).

Table II

Details of 14 fish radio-tagged in the River Tay over the period 30 April–30 May 1988. All times are GMT

Fish No	Capture		Sex	Weight (kg)	Time	Discharge				FR**	Recapture site
	date	site				at release $m^3 s^{-1}$*		at entry $m^3 s^{-1}$			
1	25/04	SG	F	6.35	1504	158	(142)	169	(161)	I	
2	26/04	SG	F	6.27	1425	169					SG (26.4)
3	28/04	SG	#	#	1234	176	(174)	162	(144)	DS	
4	30/04	SG	F	6.40	1611	141	(123)	142	(126)	I	
5	03/05	SG	F	5.50	2140	141	(120)	141	(122)	I	
6	03/05	SG	M	6.70	2025	141	(120)	141	(122)	I	
7	04/05	SG	F	5.50	1909	140	(122)	140	(122)	S	
8	04/05	SG	F	4.90	0816	140					LE (4.5)
9	09/05	SG	F	3.90	0929	104					LE (4.5)
10	25/05	SG	M	2.40	1136	81	(75)	94	(88)	I	
11	25/05	SG	M	2.00	1150	94					LE (25.5)
12	27/05	SG	F	4.10	1230	76	(61)	76	(49)	DS	
13	30/05	SPS	F	7.50	1630	72	(56.5)	72	(61)	DS	
14	30/05	SPS	F	7.90	1735	72	(59.4)	72	(60)	DS	

* MDD and instantaneous flows (in parentheses) calculated as described in Materials and Methods

** FR estimated from hydrographs recorded at Ballathie (see Materials and Methods)

# denotes a specimen whose sex and weight was not determined

Table III

Details of 17 salmon radio-tagged in the River Tay over the period 1 June–8 July 1988. All times are GMT

Fish No	Capture		Sex	Weight (kg)	Time	Discharge*				FR**	Recapture site
	date	site				at release $m^3 s^{-1}$		at entry $m^3 s^{-1}$			
15	01/06	SG	F	8.1	1726	66	(53)	66	(53)	S	
16	01/06	SG	F	5.1	2015	66				S	LE (01.6)
17	10/06	SPS	M	8.9	1130	55	(44)	95	(52)	DS	
18	10/06	SPS	M	7.3	1335	55	(43)	95	(43)	DS	
19	20/06	SPS	M	6.2	1835	45	(34)	45	(34)	S	
20	21/06	SPS	M	4.5	1927	46	(33)	46	(41)		
21	23/06	SPS	F	8.3	0954	42					MY (29.6)
22	28/06	SPS	M	4.8	1436	38	(29)	38	(28)	S	
23	29/06	SPS	M	4.3	1258	37					LE (29.6)
24	29/06	SPS	F	3.7	1657	37	(27)	37	(27)	S	
25	30/06	SPS	M	4.0	1740	37					LE (30.6)
26	30/06	SPS	M	4.9	2130	37	(27)	37	(27)	S	
27	05/07	SPS	F	3.4	1940	70					TY (06.7)
28	06/07	SPS	M	1.3	0945	70	(62)	70	(55)	DS	
29	06/07	SPS	M	4.4	1020	70	(60)	70	(55)	DS	
30	08/07	SPS	F	1.3	1045	60	(48)	60	(48)	DS	
31	08/07	SPS	F	7.2	0906	60	(48)	60	(48)	DS	

* MDD and instantaneous flows (in parentheses) calculated as described in Materials and Methods

** FR at river entry (see Materials and Methods)

Table IV

The timing of release and subsequent arrival at the Tay/Almond confluence of nine radio-tagged salmon in a period of greater than eight hours after their release time (25 April–30 June 1988). All times are GMT

Fish	Release date and time	MDD $m^3 s^{-1}$	River entry date and time	Time interval (h.m.)	MDD $m^3 s^{-1}$	% SMDD	FR*
F1	25/04; 1604	158	26/04; 1730	25.26	169	113	I
F6	03/05; 2125	140	04/05; 0744	10.19	140	111	I
F12	27/05; 1330	76.0	28/05; 1040	21.10	76	60	DS
F13	30/05; 1630	72.0	31/05; 0248	10.18	72	57	DS
F17	10/06; 1130	55.0	12/06; 0110	37.40	95	112	DS
F18	10/06; 1335	55.0	12/06; 2330	57.55	95	112	DS
F19	20/06; 1927	45.0	21/06; 0302	7.35	45	45	S
F22	28/06; 1436	38.0	29/06; 0020	9.44	38	45	S
F26	30/06; 2130	37.0	01/07; 0715	9.45	37	44	S**

* FR at river entry (see Materials and Methods)

** denotes fish that resumed movement up stream during increase in flow of the River Almond, before spate flows descending the main river had reached the estuary

Almondmouth (11 km) within eight hours of being released (Tables II and III).

The behaviour of the remaining nine fish in the same area of the upper estuary were examined over a longer time period. Details of the movements of these fish in relation to prevailing flows are shown in Table IV. Members of this group remained in the estuary over a range of instantaneous flows entering the estuary of ca 45 to 141 $m^3 s^{-1}$.

Six members of this group of fish resumed their migration up stream after or during the course of increases in main river flows entering the upper estuary (Table IV). The two exceptions, fish F19 and F22, were released during some of the lowest main river flows recorded that summer (44–54% SMDD, June). Both fish moved into the river during the next period of darkness after their release. Fish F12 and F13 continued up stream during the course of a decline in previously elevated flows associated with two small spates over 27 and 28 May (peaking at Almondmouth at ca 2300 hours on 27 May; 82.1 $m^3 s^{-1}$) and on 30 and 31 May (peaking at ca 2100 hours; 76 $m^3 s^{-1}$).

The longest delay was shown by F18, which passed the ALSTN at Scone 58 hours after being released (Tables III and IV). For much of this time the fish remained at Perth Dock. Its subsequent movement through the head of tide coincided with the first period of darkness after a small spate (peak flow; 55.3 $m^3 s^{-1}$) which had been recorded at Ballathie from midday on 11 June to the same time on the following day.

Movements from Almondmouth into the lower reaches of the river

Tables V and VI show the timing of the passage of the radio-tagged salmon from Almondmouth to Islamouth (26.5 km) during their initial penetration of the lower reaches of the river.

In general, movement up stream from the head of tide to the first stopping position was continuous and conformed to a common general pattern. Entry to the river, past the tidal limit and subsequent movement up stream associated with sustained initial penetration of the lower river was recorded over a range of seasonal flows, including flows below the seasonal norm (Fig. 2). The timing of ascent through the head of tide at Scone, past the ALSTN at Almondmouth tended to dictate the timing of subsequent movements within the lower river to the first stopping point. Fish entering the river in the early morning often continued to migrate up stream during the day (see fish F6, F12, F13, F15, F17, F19, F26, F28, F29 and F30).

The distance travelled up stream by each fish to its first stopping position in the river was variable; migrants mostly terminated their initial penetration of the lower reaches of the river between Almondmouth and Islamouth, 15.5 km further up stream. The most frequently used areas associated with the first stop in the lower river were the recognised fishing pools between Almondmouth and Stormontfield, the "Pitlochrie pool" to the weir above Stanley and from the Linn at Campsie to Islamouth (Table VII, Fig. 1).

The mean distance moved up stream from the tidal limit at Scone during the initial phase of movement by

Table V

Summary data of the timing of upstream movement of 10 radio-tagged salmon through the lower reaches of the River Tay: 24 April–31 May 1988 (inclusive). All times are GMT

Fish	Almondmouth		Fishponds		Stanely Weir		Taymount		Islamouth*	
	Date	Time	Date	Time	Date	Time	Date	Time	Date	Time
1	26/04	1730	26/04	2400	28/04	2025	30/04	1835	30/04	2130
3	28/04	1824	28/04	2235	29/04	1935	29/04	2310	10/05	1450
4	30/04	2306	-	-	-	-	-	-	-	-
5	04/05	0516	10/05	1620	-	-	11/05	2035	12/05	2236
6	04/05	0745	04/05	1105	04/05	1550	09/05	1705	05/05	1830**
7	04/05	2248	05/05	0255	05/05	0940	05/05	1810	05/05	1830
10	25/05	1728	28/05	2145	-	-	29/05	0145	29/05	0311
12	28/05	1040	28/05	1515	-	-	28/05	2300	29/05	2205**
13	31/05	0248	31/05	0525	31/05	0830	31/05	2201	01/06	0230**
14	31/05	0215	31/05	0511	31/05	2140	02/06	0151	02/06	0531

* positions of monitoring points indicated in Figure 1
** denotes those fish moving up stream during the day

Table VI

Summary data of the timing of the upstream movement of 11 radio-tagged salmon through the lower reaches of the River Tay: 2 June–8 July 1988. All times are GMT

Fish	Almondmouth		Fishponds		Stanely Weir		Taymount		Islamouth	
	Date	Time	Date	Time	Date	Time	Date	Time	Date	Time
15	02/06	0210	02/06	0510	02/06	0914	02/06	1025	02/06	1550*
17	12/06	0110	12/06	0435	12/06	1020	12/06	2310	13/06	0450*
19	21/06	0402	21/06	1025	-	-	21/06	1830	23/06	0145*
20	22/06	0204	24/06	0225	-	-	-	-	25/06	0145
22	29/06	0020	29/06	0355	29/06	0930	30/06	2231	03/07	0201
24	29/06	2136	30/06	0820	02/07	0320	02/07	0435	02/07	2055
26	01/07	0715	01/07	1045	01/07	2201	-	-	03/07	0750*
28	06/07	1420	06/07	1650	06/07	2030	06/07	2136	-	-
29	06/07	1510	06/07	1740	06/07	2200	07/07	0431	07/07	1830*
30	08/07	1604	09/07	1235	09/07	1557	09/07	1712	-	-
31	08/07	1446	08/07	2255	09/07	0246	10/07	1851	-	-

* denotes those fish moving up stream during the day.
Note. F18 was not recorded passing the five ALSTN units listed.

each of the four seasonal groups of migrants differed. In April, the average distance travelled was 5.9 km. It increased to 11.7 km in May but decreased to 7.6 km in June. The largest movements were recorded in July (13.6 km). Individual seasonal and pooled values were compared to the mean level of river flow and the proportion of the normal seasonal flow recorded at the time of passage through the tidal limit but no relationships could be discerned (Table VII).

Movements after the first stop in the lower reaches of the river

Progress up stream after the first stop took place in a stepwise fashion, migratory periods alternating with stationary, quiescent periods. Salmon were usually located in the deep pools during their quiescent phase(s). Nine fish continued to move up stream (>1 km) within 12 hours of their first stop in the river. The remaining members of the study group moved either up or down stream during the following 2–5 days.

Most fish curtailed their initial ascent below Islamouth (>0.5 km). Among these fish, subsequent movements up stream to Islamouth ranged from 1 km to 12 km (mean, 3.3 km) per migratory period. The final movement to the junction at Islamouth was usually initiated from pools at Ballathie or the viaduct at Cargill rather than from areas further down stream. Accordingly, when these final, and often smaller movements to the confluence area are removed from

Table VII

Details of the movements of 22 radio-tagged salmon from the upper Tay estuary to their first stopping position in the lower reaches of the River Tay: 26 April–10 July 1988. All distances are from the Almondmouth ALSTN (11 km, Fig. 1)

Fish no	Stopping position	Distance upstream and (km)	Range of MDD* ($m^3 s^{-1}$)	Range of % SMDD**
April				
F1	Stanley	8.6	176-162	118-108
F3	Campsie Linn	10.7	162-146	108-98
F4	Luncarty	4.2	141-151	112-120
F5	Almondmouth	0.0	140-139	111-110
May				
F6	Ballathie	14.0	140-139	111-110
F7	Islamouth	15.5	139-132	110-105
F10	Lower Redgorton	1.3	94-76	75-60
F12	Islamouth	15.5	71-65	56-52
F13	Stanley Weir	9.1	72-68	57-54
F14	Campsie Linn	10.7	69-66	55-52
F15	Islamouth	15.5	66-67	78-79
F17	Taymount	11.4	54-51	64-60
F19	Upper Taymount	12.5	45-46	53-54
June				
F20	Lower Redgorton	1.5	46-47	54-55
F22	Taymount	11.2	38-37	45-44
F24	Waulkmill	2.0	38-37	45-44
F26	Islamouth	15.5	55-52	65-61
July				
F28	Upper Taymount	12.5	63-60	95-91
F29	Ballathie	15.5	63-60	95-91
F30	Ballathie	15.5	63-109	95-164
F31	Taymount	11.0	55-109	83-164

* MDD flows during movement through the head of tide and subsequent movement within the river (see Materials and Methods)

** See Table I

Note. No data for F18

the analysis, the mean distance covered increases to 3.8 km per migratory period.

Ten of the eleven ALSTN observations of fish continuing to migrate to Islamouth after their first stop in the river were recorded during the early morning, the evening, or during the hours of darkness. The single movement that did not conform to this pattern was shown by F3. On 1 May the fish moved up stream from the lower end of the main pool at Ballathie to Islamouth in the afternoon (1450 h). This activity coincided with an increase in the river flow at Ballathie (which peaked at about 1200 h on the following day) owing to heavy rainfall in the upper reaches of the river and increased generating flows from the HEP generating station at Pitlochry dam.

Fish F4 ascended to Islamouth 43 days after entering the river (Tables II and V). The delay resulted from the fish remaining at its first stopping position at Stormontfield (15/05) for about 5 days before moving up stream to Fishponds where it remained for a further 22 days. Whilst there, its position in the river channel was located at regular intervals. For much of this period the fish was located within 5–10 m of the end of the croys on the right-hand side (west) of the river. An ALSTN was placed a short distance up stream to monitor its movements, up and down stream from after 20 May. Its behaviour was monitored by the ALSTN until 12 June. Movements by this fish (ca 100–450 m) up stream to the croys at the head of the pool were most frequently recorded in

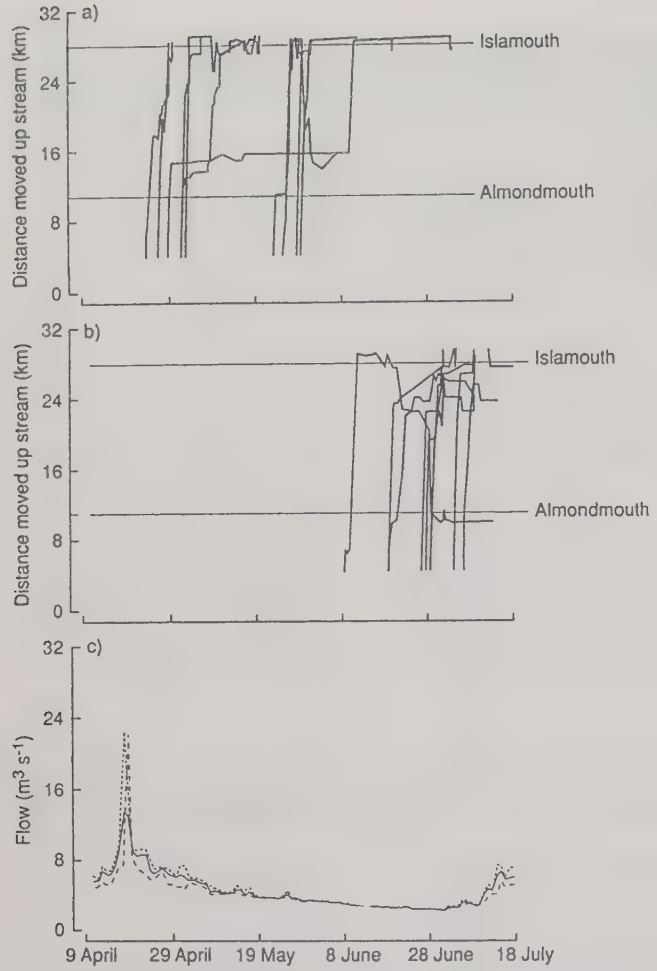

Figure 2. The movements of 20 radio-tagged Atlantic salmon (a and b) from their respective release areas, up to the area of the Tay/Isla confluence. Mean, maximum and minimum daily flows (m^3 s^{-1}) measured at Ballathie gauging station are also shown (c).

the late afternoon, at dusk and at dawn or when small spates and HEP augmented flows passed through the area. Relocations also coincided with the timing of the passage of two other radio-tagged fish. On 11 June (2320–2340 h) the fish moved up stream as another radio-tagged salmon destined for the River Tummel (see Webb, 1990) moved through the same area of the river channel. The behaviour was repeated again early in the morning of the following day (0330–0355 h) when F17 passed through the area (Tables VI and VII).

The fish resumed its upstream migration in the early hours of 12 June (0040 h) during the course of a small, short term spate (ca 21 hours duration) which passed through the area (11.6) between 1200 h and 0930 h the following day. The fish proceeded to Islamouth, whereupon it entered the middle reaches of the Tay and stopped at Kercock (30.5). It was last located near Dunkeld (46.1) at the end of October (29/10/88).

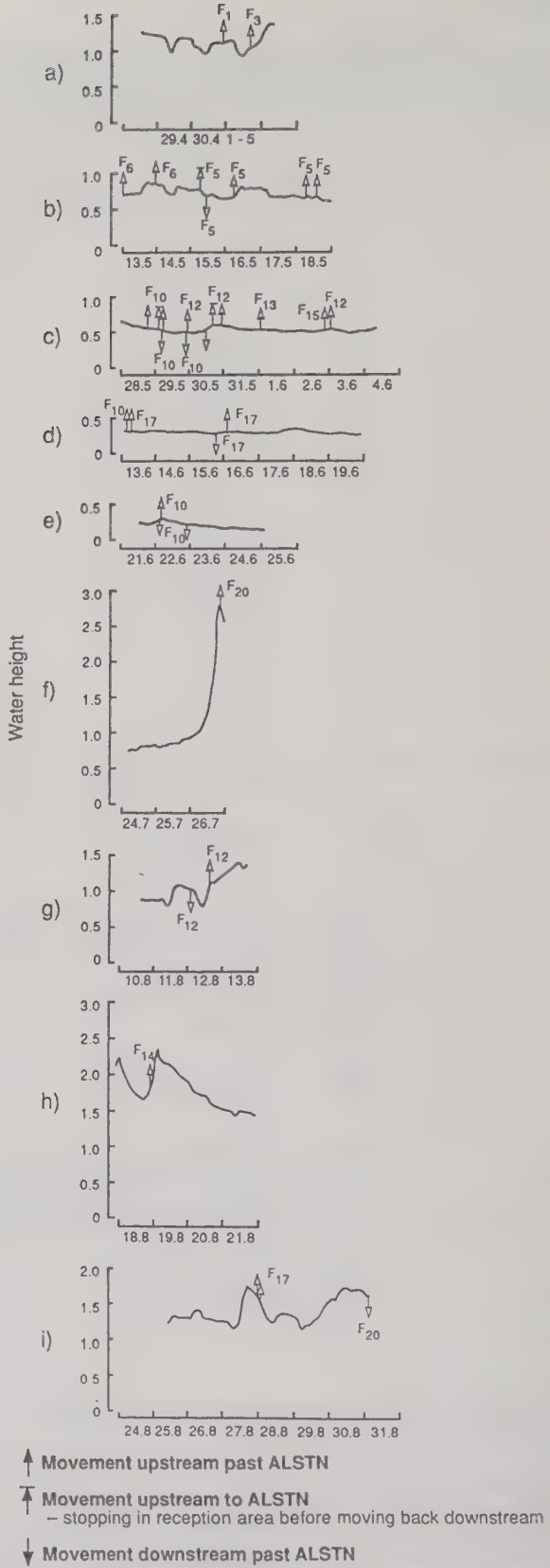

Figure 3. The timing of movements into the middle reaches of the main stem Tay in relation to simultaneous hydrographs recorded at Ballathie gauging station.

a) 29 April–1 May
b) 13–18 May
c) 28 May–4 June
d) 13–19 June
e) 21–25 June
f) 24–26 July
g) 10–13 August
h) 18–21 August
i) 24–31 August

Twenty-one of the 22 fish monitored above the tidal limit subsequently ascended to the confluence of the River Tay and the River Isla at Islamouth. Amongst the fish approaching the junction pool for the first time (excluding F28 which remained at the confluence to the end of the study period), the mean period of time spent at the confluence (between the viaduct, the Lower Isla and Meikleour house ALSTN units) was approximately 12.1 hours (range, 0.1 to 69.5 hours). Five fish remained in the area for less than 1.5 hours, suggesting that they moved through the confluence area without a delay. In contrast, nine fish remained in the junction pool area for a period of 24 hours or more.

Ten of the radio-tagged fish that migrated via Islamouth to areas within the middle and upper reaches of the River Tay and the River Isla subsequently returned to the confluence at a later date. Among this group the mean number of movements through the confluence area was 3.6 per migrant (range 2–6). There was no discernible relationship between the incidence of this behaviour and the date of entry to the river.

The timing of the first quiescent phase

For the purposes of description, the first quiescent phase corresponded to the period over which the fish ceased activity up to the end of the period that it remained in the same general area of the river (not moving up or down stream by more than 1 km) for 10 days in succession. This period varied between the monthly groups of migrants released over the study period. In late April, migrants remained active for one to 33 days (mean 19 days). In May the range was one to 20 days (mean 10.1 days), and in June the period had reduced to between one and 19 days (mean 8 days). By July, the mean and range values were reduced further to between one and six days (mean 3.6 days).

General patterns of movement

Of the 22 fish tracked higher than Almondmouth, 10 entered the middle reaches of the Tay, above the confluence of the River Isla (fish F1, F3, F5, F6, F10, F12, F13, F14, F15 and F17). Five fish were subsequently observed to move back down stream to Islamouth and to enter (and subsequently remain until spawning) the River Isla and its tributaries (fish F5, F6, F10, F12 and F20).

Fish F19 was the only tagged fish to enter the middle reaches of the Tay and remain there until spawning having entered the Isla earlier in the year (3–6 July). No radio-tagged fish was recorded to enter the River Almond.

Entry to the Lower Reaches of the River Isla

The timing of 20 movements of radio-tagged fish into the lower reaches of the River Isla through the reception area of an ALSTN positioned 2 km up stream from the confluence at Islamouth was recorded. Despite daily monitoring, tagged fish were not located between the confluence pool and the ALSTN unit. This observation suggests that all the upstream movements were initiated from either the Islamouth or other areas of the main river. Thus fish tended not to reside in the area of the lower reaches of the tributary between the confluence and the monitoring site.

Movement into the tributary from the main river was recorded over a range of tributary flows which corresponded to varying proportions of the seasonal norm. In many cases sustained entry and penetration of the tributary was associated with either increases in flow above former levels or to levels above the seasonal norm. This pattern was particularly evident between June and August when all the sustained movements into the tributary coincided with spates which often approached or were in excess of the seasonal norm (Table VIII). The distances between the two gauging stations and Islamouth (Fig. 1) prevented the appropriate summary FR codes being determined in each case.

Movements in the Middle Reaches of the River Tay

Eleven of the 21 fish that ascended to Islamouth subsequently ascended to the ALSTN at Meikleour House above Kinclaven bridge (Table IX). Thirty-three ALSTN recordings were made of the movements of radio-tagged fish past the ALSTN at Meikleour House (Table IX). The timing of their movements (up and down stream) in relation to hydrographs simultaneously recorded at Ballathie and Caputh gauging stations are shown in Figures 3a-i.

Entry (movement up stream) into the middle reaches of the Tay from Islamouth was recorded over a range of flows (27–261 m^3 s^{-1}) recorded at Ballathie corresponding to mean daily discharges of 51–314 m^3 s^{-1} (51–314% SMDD) and mean daily discharges of 35–174 m^3 s^{-1} recorded at Caputh (51–251% SMDD). Ninety-one percent of this activity coincided with an increase in the flow of the main river, or a decline in spate flows or stable flows within 24 hours of the decline of a flood event. The remaining two movements were associated with declining basal flows (Table IX; Figs 3a-i).

Figure 4 shows the timing of 62 upstream movements of radio-tagged fish between Meikleour House (29) and the confluence of the River Tay and the River Tummel at Logierait (53) recorded by ALSTN units distributed along the river bank between the two sites. The single movement recorded in August – F14

Table VIII

Summary data of the timing of the movements of radio-tagged salmon in the lower reaches of the River Isla: 22 May–1 September 1988. Details of the daily levels of flow recorded at Craighall* and Wester Cardean* gauging stations are also shown. All times are GMT

Fish	Date	Time	River Ericht* ($m^3 s^{-1}$)		River Isla* ($m^3 s^{-1}$)	
			MDD	%SDD	MDD	%SDD
F5	22/05	0101**	3.36	37.0	2.7	45.0
	22/05	0131#	3.36	37.0	2.7	45.0
	25/05	1615	7.0	72.0	4.3	71.0
F6	05/05	1800	7.5	77.0	5.4	90.0
	11/05	2256#	5.3	55.0	3.9	65.0
	21/05	–	3.4	35.0	2.6	43.0
F7	08/05	0630	7.2	74.0	5.5	92.0
F10	06/07	0554	7.5	129.0	8.2	222.0
F12	31/05	2101	6.1	63.0	3.5	58.0
	03/06	2205#	5.0	94.0	3.2	86.0
F19	03/07	2136	4.5	78.0	3.1	120.0
	06/07	1330#	5.8	100.0	4.4	169.0
	06/07	0040	8.9	153.0	8.2	315.0
		0454#	8.9	153.0	8.2	315.0
		0532**	8.9	153.0	8.2	315.0
F20	01/09	1922	38.6	330.0	48.7	974.0
F22	10/07	2058**	22.3	384.0	12.7	488.0
F24	02/07	2212	9.7	167.0	7.1	273.0
F26	14/08	1422	15.0	124.0	26.0	650.0
F29	10/07	1624**	22.2	383.0	12.7	488.0

* see Figure 1

** denotes short range excursions (*ca* 1.5-2.5 km) into the lower Isla

fish moving down stream

through an ALSTN at Meikleour from Ballathie on 19 August (0055 h) – is not shown.

Thirty-three (53%) of 62 upstream movements were recorded between sunset and sunrise. When the periods of two hours before sunset and after sunrise are included in the analysis, the number increases to 47 observations (76% of the activity recorded). Outwith these periods, seven of the remaining 15 observations coincided with river flows that were greater than the seasonal norm.

The length (km) of individual episodes of movement initiated from Islamouth (>0.5 km) was compared to flows at that time and to levels of flow recorded over the previous 24 hours in each case but no relationships were found.

During movements in the middle reaches of the river, the mean distance covered by tagged fish per migratory period (>0.5 km) ranged from 1.1 to 14.2 km (mean, 5.7 km). In May, June and July the mean distance covered per migratory period was 5.6 km, 5.32 km and 8.6 km respectively. The differences in the mean values were not statistically significant. In general, the larger distances covered were initiated from Islamouth or Murthly or movements from other areas coinciding with the higher seasonal flows. This relationship was particularly evident if in each case, the last movement up stream (>0.5 km) before the fish took up a longer term residence in a single pool (see Hawkins and Smith, 1986; Laughton 1989; Webb, 1989) was excluded from the analysis.

The most popular stopping areas within this area of the main river were in various pools at Kercock (30), Murthly (40), Dunkeld (46), Dalguise (48) and Kinnaird (52) (Fig. 1).

Table IX

Summary data of the movements of radio-tagged salmon past an ALSTN at Meikleour House. All times are GMT

Fish no	Date	Time	Ballathie discharge			Caputh discharge	
			MDD m^3s^{-1}	SMDD	FR**	MDD m^3s^{-1}	SMDD
F1	30/04	2145	142	95	I	124	104
F3	01/05	1740	152	121	I	132	129
F5	15/05	0600#	87	69	DS	84	83
	16/05	0435	87	69	I	74	73
	18/05	0430	86	68	I	71	70
	18/05	1350#	82	65	I	71	70
F6	13/05	0155	96	76	I	80	78
		2355	107	85	DS	91	89
F10	29/05	0145	71	56	DS	58	57
		0511#	71	56	DS	58	57
		0520	71	56	DS	58	57
		0535	71	56	DS	58	57
		2230#	94	74	I	53	52
	13/06	0230	51	60	D	40	59
	22/06	0250#	46	54	I	36	53
		0340	46	54	I	36	53
		2245#	45	53	DS	35	51
F12	29/05	2330	65	52	DS	53	52
	30/05	1130#	76	60	I	53	52
		1645	72	57	I	56	55
		2300	72	57	DS	56	55
	03/06	0240-0245	67	79	I	53	78
	11/08	2204#	136	159	DS	117	169
	12/08	1312	–	–	I	–	–
F13	01/06	0325	69	81	DS	54	79
F14	19/08	0055	302	352	I	174	251
F15	02/06	2245	67	79	I	54	79
F17	13/06	0305	51	60	D	40	59
	15/06	2205#	47	55	D	37	54
	16/06	0615	47	55	D	37	54
	27/08	2245-02.05	220	257	DS	153	218
F20	26/07	2350	314	474	I/DS	259	470
	31/08	1020#	219	256	DS	171	244

# denotes movement down stream
** see Materials and Methods

Movements into the Lower Reaches of the River Tummel and the Upper Reaches of the River Tay

Four of the tagged fish that entered the middle reaches of the main river from Islamouth continued to migrate further up stream and entered the lower reaches of the River Tummel and the upper reaches of the River Tay (ie above the junction at Logierait; Table X). The timing of their movements past an ALSTN positioned at the confluence in relation to hydrographs recorded at Pitnacree (Fig. 1) are shown in Figures 5a-d.

Of the 14 cases of tagged fish passing ALSTN units whilst moving up stream to the confluence or into the upper Tay or the River Tummel, nine coincided with increases in the flow of the main river or soon after (<24 hours). The remaining five movements coincided with stable flow conditions. In contrast, five of the seven downstream movements past the ALSTN

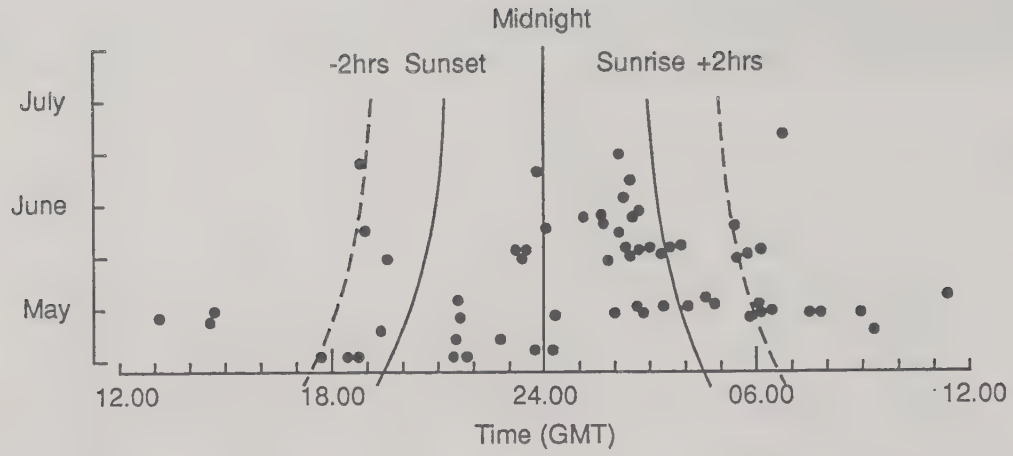

Figure 4. The time of day when fish were recorded migrating up stream in the River Tay from Islamouth to the junction of the River Tummel; each point indicates the time at which radio-tagged fish passed an ALSTN. The change in the times of sunset and sunrise are also shown.

to the confluence pool or areas below coincided with stable or declining basal flows (Table X: Figs 5a-d).

Extensive movements up and down stream

Ten fish showed extensive movements up or down stream (>5 km) within different parts of the river system some months before spawning. Figures 6 and 7 show three examples. Most of this activity was initiated from areas immediately above or below the confluence of the River Tay and the River Tummel and at Almondmouth.

Among the earlier migrants, the phenomenon was most commonly recorded in the middle and upper reaches of the Tay, the lower Tummel and the confluence area below. In contrast, fish released in June and early July showed movements of this kind in the middle and lower reaches of the main river, the lower reaches of the River Isla and the confluence at Islamouth (Fig. 7).

Movement (up or down stream) in the absence of an increase in flow above either the seasonal norm or the pertaining basal flow was restricted to nocturnal and crepuscular periods only. Movements recorded during the daylight hours tended to coincide with increases in the flow of the main river or a nearby tributary.

Final destinations of the radio-tagged fish

Fourteen of the 31 fish released over the study period were located at the end of October before spawning. Among this group, those migrants that were released in the period April to mid-June were located at greater distances up stream than fish released later in the summer (Tables XI and XII).

Discussion

In 1987 and 1988, 86 salmon were radio-tagged and released into the upper Tay estuary near Perth. Major differences were observed in the movements and spawning destinations of fish released at different times of the year. Salmon entering the river earlier in the year penetrated and spawned at greater distances from the tidal limit than those entering later. These observations accord with the results of previous radio telemetry studies conducted on other rivers including the Aberdeenshire Dee and the River Spey (Hawkins and Smith, 1986; Laughton, 1989, 1991) and with results from other field studies using different techniques in Scotland and elsewhere (Saunders, 1967; Struthers, 1984).

The likely consequences of the size and geographical complexity of the River Tay on the migratory behaviour of salmon entering the river at different times of the year have been discussed previously. The movements of adult salmon of different sea-ages homing to common natal areas of the river system tend to occur at different times of the year. In relatively simple, linear river systems one might expect fish to enter the estuary serially, fish travelling the greatest distance to their final spawning positions entering earliest. However, in more complex river systems like the Tay which may have several large drainage areas and large tributaries, there will tend to be an overlap in the timing of the movements of salmon through the estuary destined for quite different areas of the river system (Webb, 1989, 1990).

Behaviour in the Estuary

Radio-tagged fish released into the tidal fresh water upper reaches of the Tay estuary (approximately 12 km up stream of the highest point of saline intrusion)

were not recorded to move down stream over distances greater than 0.25–2.0 km from their respective release points. Furthermore, no relationship was evident between the time that tagged fish remained in the estuary and their tendency to move down stream (Webb, 1989, 1990). In view of these observations, it is probable that all of the fish taken for tagging in the upper reaches of the Tay estuary were committed to enter the river at capture. In contrast, salmon captured and released in the lower, brackish or fully saline reaches of estuaries may remain there for some time (Stasko, 1975; Potter, 1988) or move back into coastal waters (Potter, 1988) before entering a river.

River Entry

After being released, most of the tagged fish moved directly up stream. Movement from the upper reaches of the estuary and into the river was recorded over a wide range of main river flows corresponding to varying proportions of normal seasonal levels of flow. No attempt was made to establish whether there was any tendency for tagged fish to enter the river at any particular time of the day and how this might be affected by river flow.

The direct movement up stream and into fresh water observed during this study is consistent with the results reported by other workers studying the behaviour of adult salmon in rivers elsewhere (Hawkins and Smith, 1986). Despite this general pattern of upstream movement, however, some delays were recorded. Amongst delayed fish , the resumption of movement into the river (past the tidal limit) coincided with either the next period of darkness or the arrival of an increase in river flow (not necessarily above the seasonal norm) into the estuary or soon after.

Where delays have been observed in the movement of Atlantic salmon into rivers from estuaries and nearby coastal waters, they have been reported as being associated with periods of reduced river flow (Menzies, 1931; Cragg-Hine, 1985; Milner, 1989; Potter, 1988). Moreover, the resumption of migratory activity amongst delayed fish has been said to coincide with increases in the level of fresh water entering estuaries or coastal waters. These increases in flow may be either small spates above basal levels, or more commonly, larger flood events to levels exceeding the seasonal norm (Menzies, 1931; Milner, 1989; Potter, 1988).

Movement to the first stopping position in the lower reaches of the river

Many of the tagged fish, after passing through the tidal limit, moved up stream in a more or less continuous manner to their first stopping position. This behaviour was recorded amongst migrants entering the river immediately after being released and those who delayed their ascent for up to three days

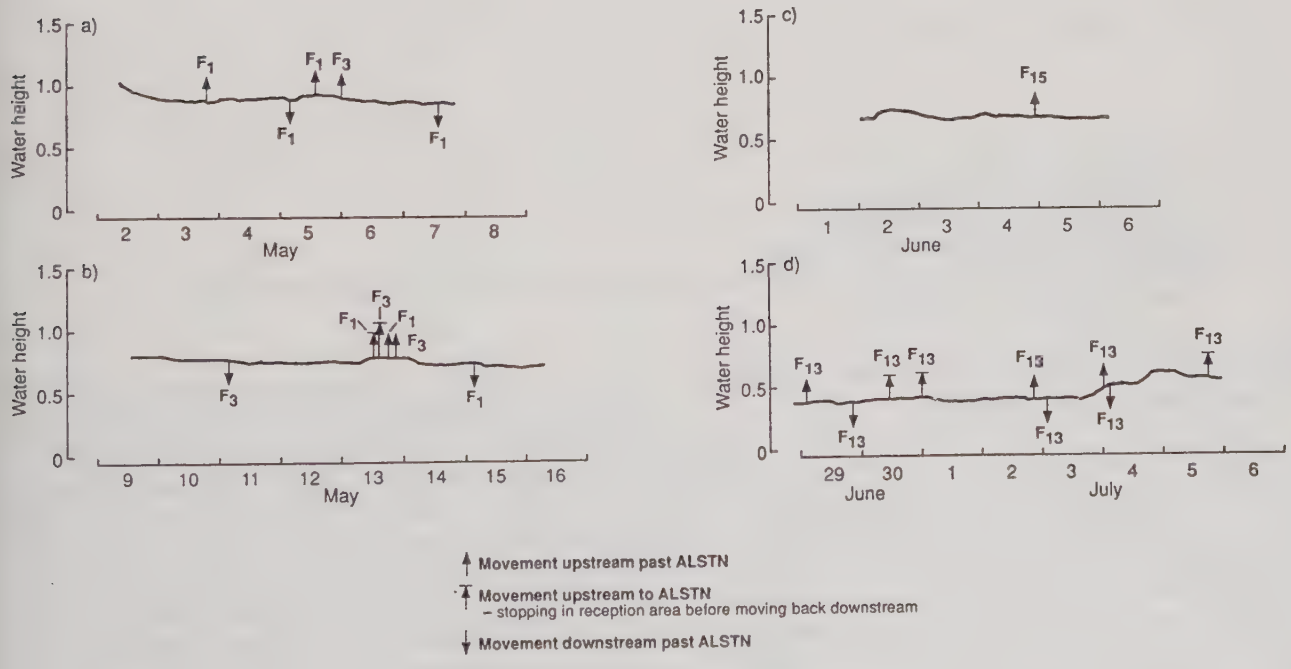

Figure 5. The timing of movements into the upper reaches of the main stem Tay in relation to simultaneous hydrographs recorded at Pitnacree gauging station.
a) 2–8 May b) 9–16 May c) 2–6 June d) 28 June–6 July

Table X

Summary of the timing of recorded movements of radio-tagged salmon in the area of the Tay/Tummel junction: May–July, 1988

Fish No	Date	Movement area	Time GMT	MDD discharge			
				Tay		Tummel	
				$m^3 s^{-1}$ +	FR*	$m^3 s^{-1}$$	FR*
F1	03/05	U Tay	1745	42.0	I	60.0	
	05/05	M Tay#	0230	43.0	S	58.0	
	05/05	Tummel	1246	44.0	I	55.6	I
	07/05	M Tay#	1354	38.0	S	55.0	
	13/05	Junction	1236	32.7	I	49.7	
		U Tay	1454	32.7	I	49.7	
	15/05	M Tay#	0144-0316	28.0	DS	42.0	
F3	05/05	U Tay	2242	43.6	DS	55.6	
	11/05	M Tay#	0322	32.0	D	39.0	
	13/05	Junction	1312	33.0	I	49.0	
		U Tay	1350	33.0	I	49.0	
F13**	28/06	U Tay	0100	8.5	S	19.0	
		M Tay#	2032	8.0	S	17.8	
	29/06	Junction	1115	8.0	S	18.0	
	30/06	Junction	0022	8.0	S	17.9	
	01/07	U Tay	2038-2254	9.6	S	18.0	
	02/07	M Tay#	0230	9.6	S	18.0	
	03/07	U Tay	0116	15.2	I	17.6	
		M Tay#	0440	15.2	I	17.6	
	04/07	Junction	1934-2058	17.4	DS	13.6	
F15	05/06	U Tay	0118	20.1	S	22.1	

\+ measured at Pitnacree (Fig. 1)
$ measured at Port-na-Craig (Fig. 1)
\# denotes downstream movement
** behaviour continued until 25 August
* estimated from hydrographs recorded at Pitnacree and Port-na-Craig gauging stations (see Materials and Methods)

(see Webb, 1989) and was recorded over a wide range of river flows and times of day.

Ascent through the tidal limit and into the lower reaches of the river was often both rapid and sustained. In many cases, this migratory activity continued for up to 24 hours, over which time many fish moved up stream to their first stopping position in the river, often between 4–15 km from the head of tide. Fish entering the river early in the morning often continued to migrate up stream during the following day to their first stopping position in the lower river.

A period of sustained movement up stream from tidal waters into fresh water above the tidal limit appears to be characteristic of the behaviour of adult salmon entering some of the larger rivers on the east coast of Scotland (Webb, 1990). The phenomenon has also been observed amongst many of the salmon that have been tagged and released in the estuary at Aberdeen that subsequently entered the River Dee (Hawkins and Smith, 1986). However, sustained movement has not been so commonplace amongst fish tagged and released above the tidal limit in a study on the River Spey (Laughton, 1989, 1991). These observations suggest that sustained movement is unlikely to be the

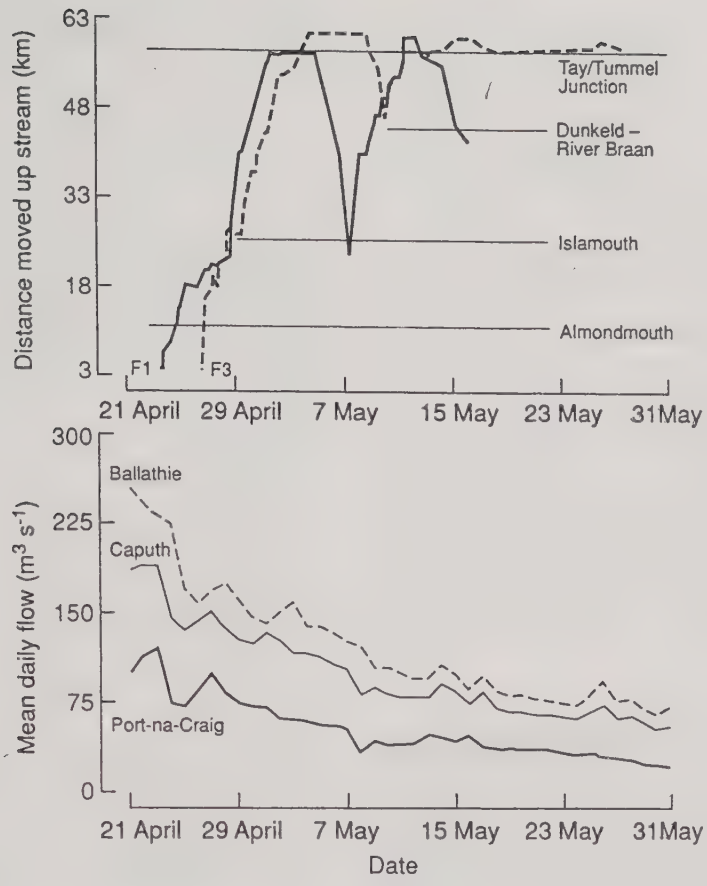

Figure 6. The movements of F1 and F3 within the mainstem Tay and the River Tummel. Mean daily flows recorded at Ballathie, Caputh and Port-na-Craig gauging stations are also shown.

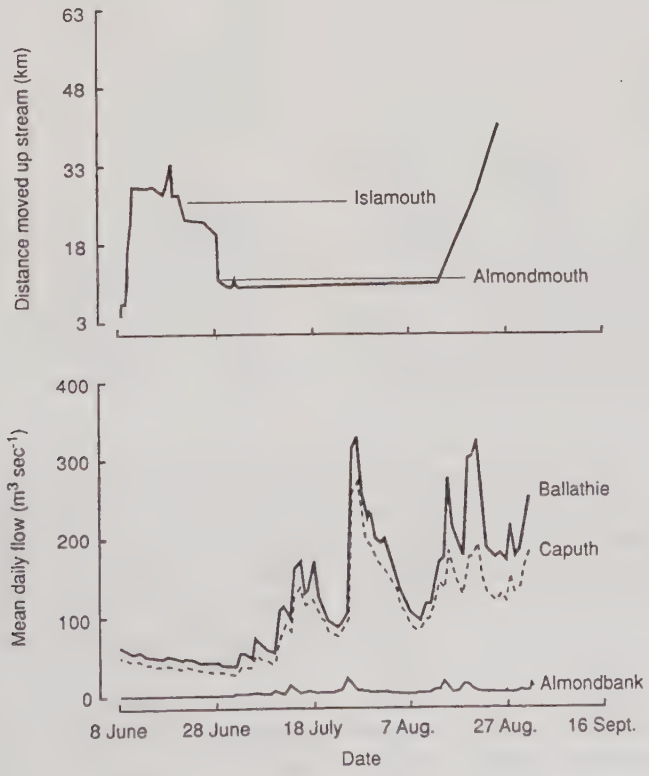

Figure 7. The movements of F17 within the mainstem Tay. Mean daily flows recorded at Ballathie, Caputh and Almondbank gauging stations are also shown.

Table XI

Summary data of the movements of salmon radio-tagged and released into the River Tay: 26 April–31 May 1988

Fish No	Date of river entry	Date of last observation	No days tracked	Last recorded position	Distance up stream (km)
1	26/04	06/09	134	River Tay (Kinnaird)	56.0
3	28/04	29/10	185	River Tay (Upper)	71.9
4	30/04	29/10	183	River Tay (Dunkeld)	46.1
5	04/05	29/10	179	River Shee	77.5
6	04/05	01/06	29	River Ericht	42.0
7	04/05	29/10	179	River Ardle	81.0
10	25/05	06/09	105	River Ericht	58.0
12	28/05	06/09	102	River Isla	39.5
13	31/05	06/09	99	River Tay	60.6
14	31/05	29/10	152	River Tay (Dalguise)	54.0

Table XII

Summary data of the movements of salmon radio-tagged and released into the River Tay: 2 June–8 July 1988

Fish No	Date of river entry	Date of last observation	No days tracked	Last recorded position	Distance up stream (km)
15	02/06	29/10	150	River Lyon	85.0
17	12/06	06/09	87	River Tay (Kercock)	30.2
18	*	29/10	–	River Tay (Kinnaird)	52.0
19	21/06	06/09	78	River Tay (Murthly)	41.5
20	22/06	29/10	130	River Ericht	46.0
22	29/06	29/10	122	River Ericht	57.0
24	29/06	29/10	122	River Shee	61.0
26	01/07	29/10	121	River Ericht	51.0
28	06/07	29/10	116	River Tay (Islamouth)	26.5
29	06/07	29/10	116	River Ardle	61.2
30	08/07	29/10	114	River Tay	29.5
31	08/07	15/07	8**	River Tay (Ballathie)	25.6

* date of river entry not known

** denotes fish caught by an angler fishing at Ballathie on 15 July

result of handling and tagging. Furthermore, the fact that movement is often recorded during the daylight hours over a wide range of flows suggests that such behaviour is characteristic of the movement of adult salmon moving into rivers from tidal waters (whether saline, brackish or fresh water). Arguably, it may therefore reflect the final stage of the marine behaviour of the adult salmon.

Many factors may affect the behaviour of salmon entering rivers. In larger rivers, levels of fresh water flow may stimulate upstream migration from an estuary without necessarily affecting subsequent activity within the river to the first stopping position (Webb, 1990). The distance up stream penetrated by migrants during this initial active phase may depend on water temperature and the positions of physical barriers and tributary confluence areas. Furthermore, the presence of a barrier in the lower reaches of a river may terminate this behaviour prematurely.

Larger initial distances tend to be covered by migrants entering rivers in the early summer months – particularly early running grilse (Webb, 1989). In contrast, fish entering the river later in the year tend to terminate their movement at or very near to their

spawning position in the lower reaches of the river (Hawkins and Smith, 1986; Webb, 1989).

Relationships between Flow and Migratory Activity

Upstream migration within the main river was recorded over a range of seasonal flows. Between late April to the middle of May, most of the migratory activity took place during a steady decline in seasonal basal flows from winter levels. Superimposed on the declining baseline of the hydrograph were regular daily increases in discharge of varying size owing to the routine operation of HEP generating facilities, together with periodic episodes of snow-melt and rainfall in different areas of the river system. Attempts to associate the movements of tagged fish with particular levels of flow or changes in flow were hampered by the considerable variation in the size and duration of the flood events in any 24 hour period. This problem was compounded by the highly variable timing of the passage of these daily increases in flow through the middle and lower reaches of the main river. Furthermore, in many instances, no single group of migrants could be identified as following a common migratory route. This prevented independent comparisons of the movements of tagged fish through common areas of the river system at different levels of flow (see Webb, 1990).

Many unregulated rivers tend to remain at or below the seasonal norm for a greater proportion of the migratory season than do large rivers affected by storage and release like much of the Tay. Perhaps, as a consequence, the most obvious relationships between changes in river flow and migratory activity were recorded amongst migrants entering the lesser or wholly unregulated tributaries of the Tay system, eg the upper Tay or the lower reaches of the River Isla.

The Tay has two unique characteristics, namely, its size and the extent to which its flows are regulated artificially. Accordingly, care should be taken in attempting to compare the data obtained during studies on the Tay with the behaviour of radio-tagged salmon elsewhere. One consequence of HEP developments on the Tay has been the creation of storage capacity. Water stored in the various reservoirs scattered throughout the drainage area is released throughout the year in a controlled way. This in turn leads to a comparatively high level of minimum flow (Pontin and Reid, 1974/1975). During the summer months, the SMDD values calculated for the period 1958–1987 tend to represent an over-estimation of the seasonal flows that might normally be expected to occur in a river of this size in Scotland. The SMDD values for the Ballathie gauging station (1952–1957, inclusive) before the development of HEP were as follows:

	Jan	Feb	Mar	Apr	May	June
SMDD	212	190	167	115	100	62
Factor	1.13	1.1	1.23	1.29	1.26	1.37

	Jul	Aug	Sept	Oct	Nov	Dec
SMDD	71	93	129	173	211	332
Factor	0.93	0.92	0.93	1.1	1.0	0.7

It is apparent that the SMDD values quoted today for the Tay vary by 92–137% of the values that would have been expected in a river of this size. Thus, in June, the seasonal mean flows may be augmented by as much as 37%. This phenomenon is likely to influence all the seasonal summaries of the gauging stations on the main river affected by the development of HEP (Table I). The effect of these enhanced, regulated flows during the summer months is not easily determined.

Long Range Excursions between Tributary Confluence Areas

Migrants were observed moving up and down stream over distances up to 30 km. In many cases the behaviour was initiated and terminated near tributary confluence areas. Among fish entering the river in late spring, the behaviour was generally recorded up to the junction of the River Tummel at Logierait, the River Braan at Dunkeld, and at Islamouth. In contrast, fish entering the river later in the study period tended to restrict their behaviour of this kind to the area between Murthly, the lower reaches of the River Isla and Almondmouth.

Webb (1989) reported broadly similar behaviour amongst radio-tagged grilse entering the Tay in the summer months. The author suggested that the phenomenon may be indicative of exploratory behaviour on the part of the fish involved. Thus it appears that migrants entering the river earlier in the year appear to exhibit the behaviour further up stream within the river system than do later entrants – an observation consistent with the relationship between time of river entry and spawning location described by Calderwood (1909), Saunders (1967), Struthers (1984), Hawkins and Smith (1986) and Laughton (1989).

Localised, exploratory movements of this kind have been reported by other workers using radio-tracking on the Dee and the Spey (Hawkins and Smith, 1986; Laughton, 1989, 1991). However, in many of these instances the behaviour may reflect the varying holding characteristics of many tributaries and different areas of the nearby main river during the summer months. However, this seems to be an unlikely explanation for some of the activity recorded in the Tay. Webb (1989) suggested that the behaviour may be indicative of exploratory behaviour. The great size of much of the main river and its principle

tributaries probably allows greater scope for activity of this kind than does any other river in the British Isles.

Concluding Comments

It is highly probable that much of the behaviour of adult salmon in rivers is determined by the date at which fish enter the river and the position within the river system at which they finally spawn. Consequently, any detailed study of the behaviour of adult salmon in a river in relation to particular environmental variables (for example, river flow) should be undertaken on the basis of a thorough understanding of these underlying variables in the river under study.

In a large and complicated river like the Tay, it is unlikely that radio-tagging small numbers of salmon or migratory trout (*Salmo trutta* L.) will provide sufficiently detailed data to estimate what levels of seasonal flow are preferred by migrants entering the river at different times of the year. For this purpose, data from longer term studies using fish counters positioned near to the head of tide of rivers may provide more useful data. Nevertheless, in this instance, the use of radio-tracking has yielded much useful data on the behaviour of salmon in the largest river in the British Isles.

Summary

The movements of 22 radio-tagged salmon ascending the River Tay and its tributaries are described. The study was undertaken over the period April to October 1988. Fish caught by sweep net in the estuary were returned to the river after conventional tagging and the insertion of a radio-tag.

Observations were made by a combination of active tracking along the river bank with a hand-held receiver and the placement of automatic listening stations at selected bankside locations. Entry to the river and subsequent upstream migration were recorded over a wide range of main stem and tributary flows. After entry to the river, movement up stream (in the absence of a spate) was limited to nocturnal or crepuscular periods only. Sustained movement into tributaries often coincided with increases in flow.

Three pre-spawning phases of riverine migratory behaviour were identified and described. Some fish moved extensively up and down stream.

Fourteen fish were continuously located up to the beginning of spawning. Fish that entered the river earlier in the season tended to spawn at sites at greater distance from the tidal limit than fish entering later in the migratory season.

The effect of flow and other factors on the migratory behaviour of adult salmon in the River Tay is discussed.

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